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Immature stages of *Calycopis caulonia* (Hewitson, 1877) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), with notes on rearing detritivorous hairstreaks on artificial diet

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Abstract

Details of egg, larval, and pupal morphology are described and illustrated for *Calycopis caulonia* (Hewitson). In particular, larval chaetotaxy is documented for the first time in *Calycopis*. Lab methods for inducing wild-caught *Calycopis* females to lay eggs and for rearing larvae on artificial diet are reported. These methods may be useful in several ways in resolving the basic taxonomy of *Calycopis*. Evidence concerning detritivory and myrmecophily in *C. caulonia* is discussed.

Key words: Lycaenidae, Theclinae, Eumaeini, *Calycopis*, systematics, life history, biology, detritivory, myrmecophily, artificial diet, rearing

Introduction

Egg, larval, and pupal morphology of Neotropical hairstreak butterflies (Lycaenidae, Theclinae, Eumaeini) remains poorly known even though the taxonomic usefulness of morphological features of the early stages in determining and understanding evolutionary patterns has long been known (see contributions in Stehr 1987). Fragmentary larval food plant information is available for about 25% of eumaeine species (Robbins unpubl.), but comprehensive life history information that can be used on a comparative basis is lacking (Duarte 2003; Duarte in prep.). Our poor knowledge of eumaeine immatures is directly attributable to the paucity of material deposited in the world's major museums and the difficulty in finding the early stages.

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Eliot (1973) overviewed lycaenid egg, larval, and pupal characters. He included three characters of the immature stages in his tentative and non-cladistic phylogeny of the family: (1) larva onisciform *vs.* differently shaped; (2) larva feeding exclusively on green plants *vs.* eating a different diet (e.g., carnivorous or eating lichens); and (3) pupa girdled or reclining *vs.* ungirdled. Downey and Allyn (1973, 1978, 1981, 1984a) described the egg and pupal ultrastructure of some eumaeines using scanning electron microscope. Although focusing on the North American fauna, Ballmer and Pratt (1988, 1992) described larval morphology of seven primarily Neotropical eumaeine genera—*Arawacus* Kaye, *Atlides* Hübner, *Chlorostrymon* Clench, *Cyanophrys* Clench, *Erora* Scudder, *Eumaeus* Hübner, *Ministrymon* Clench, and *Strymon* Hübner.

Eumaeine immature stages are not readily found in the field. Eggs are usually smaller than a millimeter in diameter (Downey & Allyn 1981, 1984a), and larvae are cryptically colored and/or feed in concealed sites. Some feed inside plant structures, such as flower buds, fruits, and succulent leaves (Ziegler & Escalante 1964; Silva *et al.* 1968; Brown 1983; Otero & Marigo 1990); some are concealed under dead leaves on the ground (Duarte unpubl.); and some are the same color as the plant part they are eating (Orsak & Whitman 1987; Monteiro 1991). Pupae usually are camouflaged and motionless, and sometimes occur inside plant fruits (Kendall 1975).

Butterflies reared from eggs in the lab are a rich source of taxonomic information. For example, (i) ontogenetic changes in coloration, morphology and behavior can be compared with other species; (ii) adult phenotypic plasticity can be determined from rearing under controlled conditions of temperature, photoperiod and humidity, which allows a more accurate characterization of species variability; and (iii) males and females can be associated correctly, which is otherwise difficult in some groups of Eumaeini (Robbins 2004a).

Calycopis caulonia (Hewitson) (Figs. 1–4) is one of the most common eumaeine species in the forested lowlands of South America south of 15°S. Field (1967) distinguished three sympatric species in the *C. caulonia* group primarily on the basis of wing pattern differences. However, we had great difficulty recognizing these species using his characters because they are highly variable. Further, although K. Johnson *et al.* (1988: 9) suggested that *C. caulonia* is "monophenic," we reared the three species that Field (1967) had recognized in the *C. caulonia* group from one female using different temperature regimes in the lab (Duarte in prep.). For these reasons, we treat these phenotypes as one species.

The biology and external morphology of the immatures of *Calycopis* Scudder are unknown for the vast majority of its 74 currently recognized species (*sensu* Robbins 2004b). Life histories have been published for *C. cecrops* (Fabricius) and *C. isobeon* (Butler & H. Druce) (Rawson & Hessel 1951; Downey & Allyn 1981; Gifford & Opler 1983; S. Johnson 1985). The most unusual features reported for these species are that adult females oviposit on dead leaves on the ground (Gifford & Opler 1983; S. Johnson 1985) and the caterpillars eat detritus (S. Johnson 1985).

FIGURES 1–4. *Calycopis caulonia*, adult. 1–2. Male, dorsal and ventral views, respectively. 3–4. Female, *idem*. Male forewing length 13 mm, female forewing length 15 mm.

The primary purposes of this paper are to describe the morphology of the immatures of *C. caulonia*, to document its detritivorous life history, and to compare our results with those for *C. cecrops* and *C. isobeon*. We also report an efficient lab method for inducing *Calycopis* females to oviposit in the lab and for rearing larvae on artificial diet. Finally, we supplement the lab results with behavioral observations of oviposition in the field.

Materials and methods

Study Site. Females of *C. caulonia* were collected in the municipality of Guapimirim, state of Rio de Janeiro, southeastern Brazil (22° 32'S and 42° 59'W, elevation 50 m) (Fig. 5). The area is located a few kilometers from Serra dos Órgãos National Park (described in more detail in Duarte *et al.* 2001 and Caldas & Robbins 2003). Adult females were collected between 20 and 30 December 1997.

Rearing Procedure. Adult females were confined individually in open translucent plastic containers about 85 mm in diameter and 110 mm deep. Dead leaves (Fig. 6) were placed at the bottom of each container and were replaced daily whether or not eggs were

laid. The containers were covered tightly with fine nylon (commercially available women's stockings) to facilitate air circulation. Temperature varied between 21° and 23° C. The butterflies were offered cotton-balls saturated with a 10% honey: water solution three times a day. If the butterfly did not extend its proboscis, we carefully uncoiled it with a fine insect pin. Eggs were collected daily (*ca.* 1800 h) and were incubated in standard Petri dishes, which were individually labeled with the oviposition date and the "number" of the mother. Small pieces of damp filter paper were placed on the bottom of the dishes to prevent desiccation. A total of 174 eggs was obtained. Newly hatched caterpillars were transferred to transparent plastic containers about 70 mm in diameter and 50 mm deep (one larva per container). Cannibalism may occur if *Calycopis* larvae are reared together (Duarte unpubl.). Sufficient artificial diet was added for larvae to eat *ad libitum*. The artificial diet was changed daily. Special care was used for first instars. They are small with fragile mouth parts, and despite our best efforts, a few "drowned" in the diet.

FIGURE 5. Map showing the collection site in the State of Rio de Janeiro, Brazil (filled area—Municipality of Guapimirim).

Artificial diet. The artificial diet used to feed larvae of *C. caulonia* was developed for *Manduca sexta* (Linnaeus) (Lepidoptera, Sphingidae), and modified by Troetschler *et al.* (1985) for *Pieris rapae* (Linnaeus) (Lepidoptera, Pieridae). We omitted formaldehyde from the original recipe because it can be harmful to insect development, even in small quantities (Vanderzant 1974). The diet ingredients and quantities needed to fill a Petri dish

(90 mm diameter and 15 mm deep) are summarized in Table 1. The diet protocol was as follows:

STEP 1—The first 10 ingredients of the diet were put in a clean beaker and mixed with 37.5 ml hot water (50° to 70° C).

STEP 2—The agar was mixed separately from the other ingredients with 37.5 ml water, until it had a smooth consistency. The water-agar mixture was heated 5-8 minutes in a microwave oven set on maximum power (setting 10). Afterwards, the mixture was stirred and heated for approximately 5 minutes (set on power 6 out of 10). This step was repeated at short intervals (20 seconds or less) until the mixture was transparent. If the mixture was translucent, it would not gel.

STEP 3—We added the mixture from step # 1 and streptomycin sulfate to the agar from step # 2, and stirred vigorously. When blended, it was poured in the bottom half of a Petri dish. The Petri dishes were refrigerated until the diet solidified, usually a few hours. Refrigerated dishes remained free of evident microorganisms for a week.

TABLE 1. Artificial diet used to feed larvae of *C. caulonia*. Modified from Troetschler *et al.* (1985).

Ingredients	Amount
1. Wheat germ	6.0 g
2. Casein	2.7 g
3. Sucrose	2.4 g
4. Salt mixture (Wesson's)[1]	0.9 g
5. Dried yeast	1.2 g
6. Cholesterol	0.26 g
7. Sorbic acid	0.15 g
8. Ascorbic acid	0.3 g
9. Vitamin mix (Vanderzant's)[1]	1.05 g
10. Linseed oil (raw)	0.3 ml
11. Water to dissolve previous ingredients	37.5 ml (50–70°C)
12. Agar	1.5 g
13. Water to dissolve agar	37.5 ml
14. Streptomycin sulfate	0.01 g

[1] For details see Parra (1996).

Rearing environment. Minimum (MN) and maximum (MX) temperatures and relative humidity (RH) were recorded daily from 8 January to 3 March 1998. We recorded the MN and MX at 1800 h, and the RH at 1000, 1400, and 1800 h. These abiotic data are available upon request from the senior author.

Statistics. Mean, standard deviation, and number of individuals are represented by the abbreviations X, SD and N, respectively. Means and standard deviations of development times for each immature stage, larval instar, and egg to adult interval were calculated. Differences between male and female development times were analyzed with a T-test at a 0.05 significance level (ZAR 1984).

Preservation of the immatures. Eggs and pupae of *C. caulonia* were photographed (to document color patterns) and then frozen for 24 hours. Larvae were photographed and then placed in hot water (*ca.* 80° C), where they remained until the water cooled. The immatures were than transferred to Kahle's solution (Peterson 1962) for 48 to 72 hours (larger specimens needed more time in the solution). Finally, all specimens were preserved in 70% ethanol.

Microscopy. Morphology of the immature stages of *C. caulonia* was studied with a light stereo-microscope and with a scanning electron microscope (SEM AMRAY 1810). Preparation for SEM analyses followed standard techniques (details in Duarte *et al.* 2001). At least five eggs, five specimens of each instar, and five pupae were examined with SEM.

Terminology. For description of the morphology of the immature stages, we followed the terminology of Downey and Allyn (1981, 1984a) for the ultrastructure of the egg; Hinton (1946) and Stehr (1987) for the chaetotaxy of the larval head capsule; Peterson (1962) for the chaetotaxy of the larval labrum; Hinton (1946), Downey and Allyn (1984b), Stehr (1987), and Ballmer and Pratt (1992) for the chaetotaxy of the larval thorax and abdomen; Lawrence and Downey (1966), Downey and Allyn (1979) for the general morphology of the larvae; and Mosher (1916) and Casagrande (1979) for general morphology of the pupa.

Vouchers. Five voucher specimens of each immature stage of *C. caulonia* are deposited in the Coleção de Lepidoptera, Museu de Zoologia, Universidade de São Paulo, SP, Brazil, and in the Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Description of the immature stages

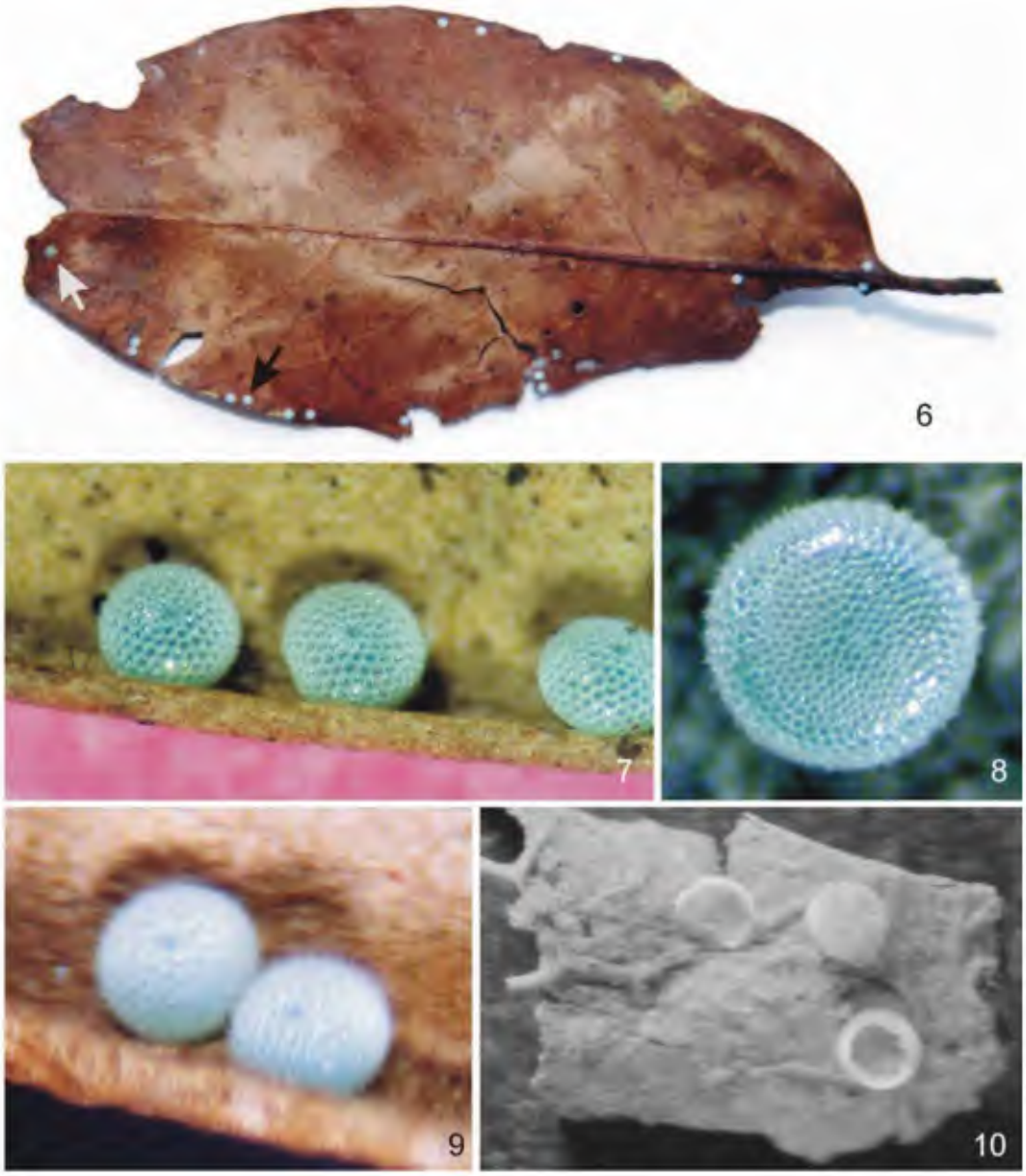
Egg (Figs. 6–18). Color greenish-blue when laid (Fig. 6), changing to whitish before hatching (Fig. 9). Exochorion whitish throughout embryonic development. Egg upright, dome-shaped, and sculptured—typical of eumaeines. Rounded in dorsal view (Figs. 6, 11), echinoid laterally (Figs. 7, 12), with upper surface convex and bottom surface (affixed to substrate) flattened (Figs. 8, 13). Micropylar area slightly depressed with rosette of four to six petal-shaped cells without ribs at base (Figs. 14–16). Rosette surrounded by three adjacent rows of cells that constitute the annulus. Chorionic thickenings and "islands" frequently protrude from "floor" of rosette cells (terminology *sensu* Downey & Allyn 1981) (Figs. 15–16). Unlike *Calycopis cecrops* (Fabricius) with "islands" only at inner part of cell (see Fig. 63 in Downey & Allyn 1981: 29), *C. caulonia* with "islands" at inner

and outer part of rosette cells (Fig. 16). Six micropylar openings. Six-sided depression (hexagon) at center of micropylar area (Fig. 16). Central micropylar area (and number of "openings") unclear in a few cases, as also reported by Downey and Allyn (1979, 1980, 1981, 1984a) (Figs. 14–15). Distinct echinoid appearance of lateral chorion produced by elongate and spine-like protuberances (= tubercles *sensu* Downey & Allyn 1981: 9) at rib intersections (Fig. 17). Protuberances with tiny aeropyle on top (Fig. 17). Besides protuberances, exochorion sculptured with pentagonal and hexagonal cells outlined by intersected carinate ribs (Fig. 18). Cells cup-shaped internally, average 50.62 µm wide at mouth (SD = 6.52, N = 11) and 21.47 µm wide at base (SD = 3.57, N = 11). Egg geometric pattern of *C. caulonia* resembles that of *C. isobeon* and *C. cecrops* (see Downey & Allyn 1981). First instar larva may eat the chorion partially or entirely (Fig. 10).

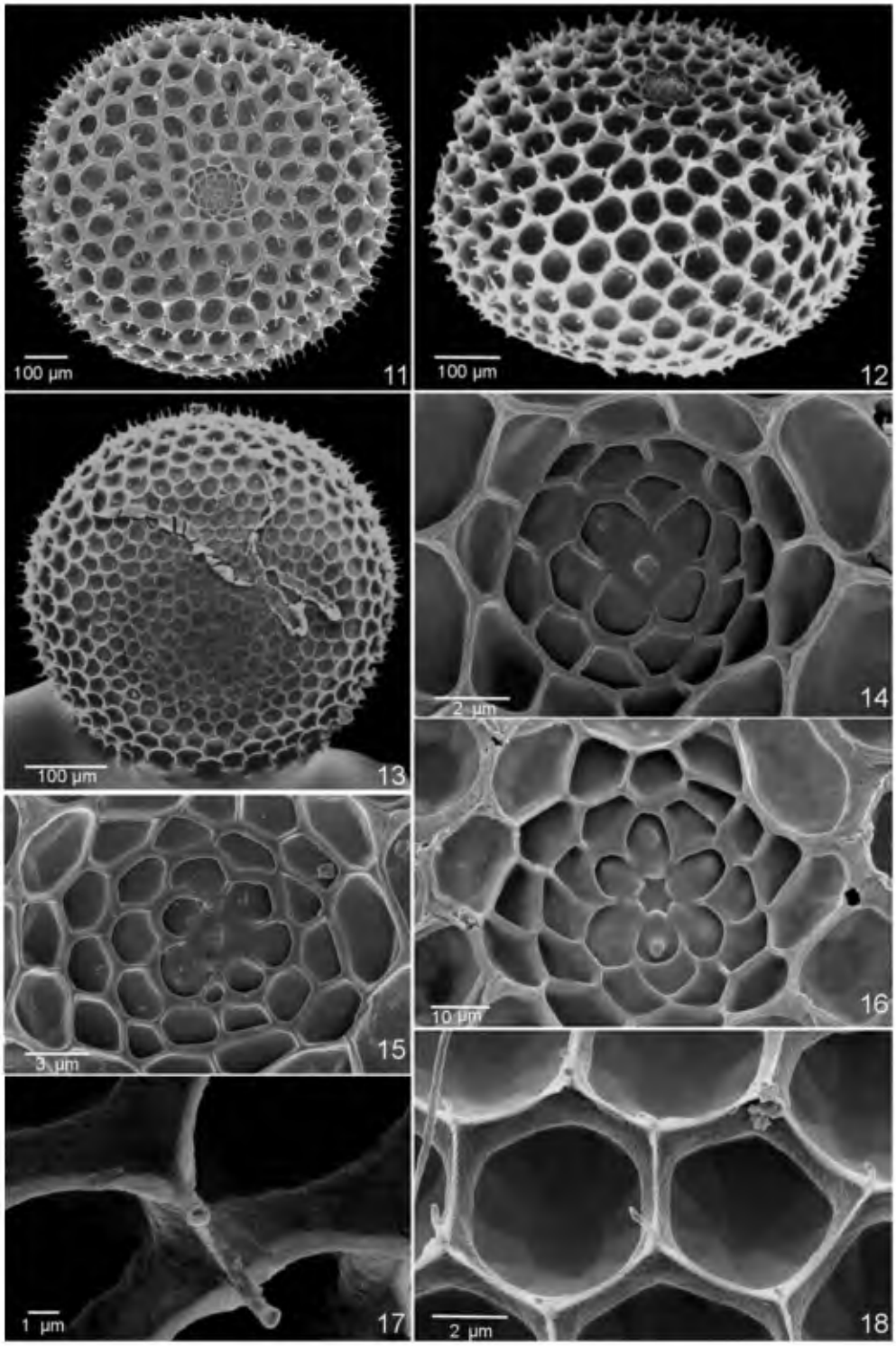
Diameter 0.54–0.58 mm (X = 0.56 mm, SD = 0.01, N = 10); height 0.25–0.35 mm (X = 0.31 mm, SD = 0.03, N = 10). Duration 4–7 days (X = 4.6 days, SD = 1.0, N = 89).

First instar (Figs. 19, 27–32, 37–44). Head wider than long; hypognathous projected; dark brown anteriorly, lighter near vertex (= epicranial notch *sensu* Stehr 1987); with tiny to very long setae (see details on larval chaetotaxy); can be retracted into prothorax. Membranous anteclypeus separates frontoclypeus from bilobed labrum. Both labrum and mandibles lighter than rest of head capsule. Mandible with eight teeth, seven visible externally, one located internally (Figs. 42–44); two mandibular setae, one nearer condyle; other distal, about 2 ½ length of former (Figs. 42–44). Length of frontoclypeus, laterally delimited by adfrontal suture, about four times length of epicranial suture (Fig. 27). Ecdysial line and adfrontal area absent in all but last instar. Larvae with six blackish stemmata on each side of head. Arrangement of stemmata as follows (Fig. 28): stemmata 1–4 in semicircle; stemma 5 ventral and adjacent to antennal socket; stemma 6 horizontally aligned with stemma 4, and more dorsal than stemma 5. Stemmata 1 and 6 nearly equal in size (mean diameter 32 µm), as stemmata 2 and 6 (mean diameter 18 µm), and stemmata 4 and 5 (mean diameter 20 µm). Body onisciform (Figs. 19, 37), light yellowish-green at emergence, and translucent-yellow after first feeding. A strongly wrinkled integument with numerous crenulations covering most of outer surface (Figs. 37–41). With exception of prothoracic seta SD1, which arises from a pinaculum (Fig. 39), each seta on larval integument supported by conical chalaza (Figs. 38–39), invariably light brown in all instars, with longitudinal ridges resembling buttresses, basally prominent and fused with cuticle. Each thoracic segment with a pair of true legs. Prothorax (T1) differs from meso- (T2) and metathorax (T3) by a pair of spiracles and a large pentagonal, prothoracic shield (Figs. 30, 32, 38). Prothoracic spiracles on each side of posterior edge of T1; larger, distinctly more ventral, and more protuberant than abdominal spiracles (Fig. 30). Abdomen with 10 segments (A1–10), distinguished by chaetotaxy (Fig. 30) and other structures. Segments A3–6 and A10 with pair of prolegs with uniordinal crochets in uniserial mesoseries, interrupted near center by conspicuous fleshy pad. Number of crochets invariant only in first instar. A3–6 with mesoseries separated into anterior and

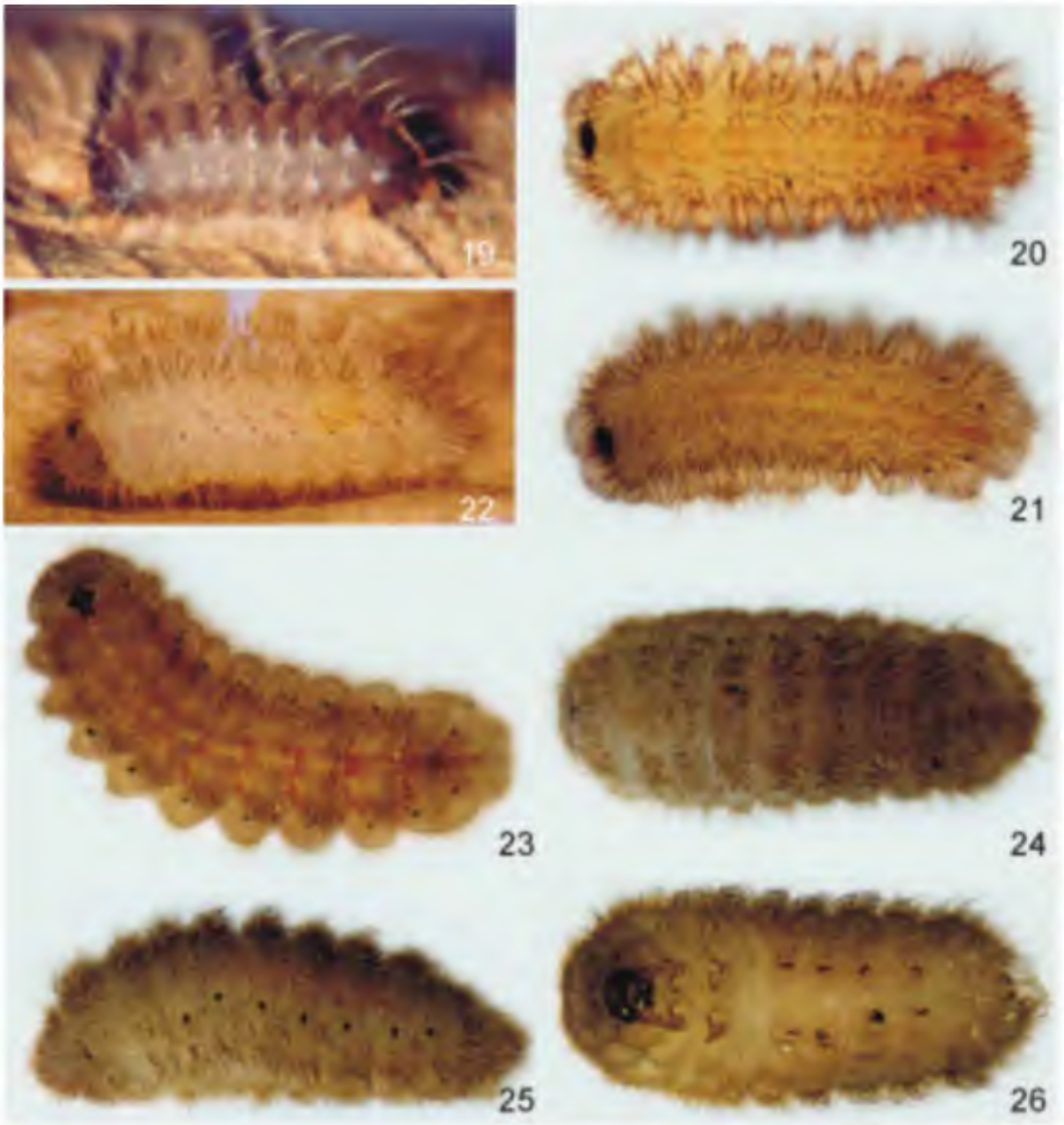
posterior groups of two crochets each. Segment A10 with single crochet postero-medially. Spiracles on A1–8, slightly anterior of segment midpoint. A1–7 spiracles co-linear, A8 more dorsal. A10 with pair of prolegs and a grayish, lanceolate, and glabrous suranal shield (present only in first instar larvae) (Fig. 31).



FIGURES 6–10. *Calycopis caulonia*, egg. 6. Oviposition on a dead leaf. Note that there are eggs (black arrow) and egg-like mold (white arrow). 7. Newly laid eggs, dorso-lateral view. 8. Ventral view. 9. Mature eggs (with less greenish blue), dorsal view. 10. Hatched eggs.



FIGURES 11–18. *Calycopis caulonia*, egg. 11. Dorsal view. 12. Dorso-lateral view. 13. Ventral view. 14. Micropylar area (rosette with four cells). 15. Micropylar area (rosette with five cells). 16. Micropylar area (rosette with six cells). 17. Spine-like protuberances with tiny aeropyles on top. 18. Cup-shaped cells (pentagonal and hexagonal) of the exochorion.



FIGURES 19–26. *Calycopis caulonia*, larva. 19. First instar preparing to molting, dorso-lateral view. 20. Second instar, dorsal view. 21. Third instar, dorsal view. 22. Fourth instar, dorso-lateral view. 23. Fifth instar, dorsal view. 24. Fifth instar preparing to molting, dorsal view. 25. *Idem*, lateral view. 26. *Idem*, ventral view.

Head capsule width 0.18–0.23 mm (X = 0.19 mm, SD = 0.01, N = 40). Body length at molting 0.83–1.23 mm (X = 1.04 mm, SD = 0.13, N = 16). Duration 3–8 days (X = 4.9 days, SD = 1.1, N = 83).

Head chaetotaxy (Figs. 27–28). *Calycopis caulonia* with 16 pairs of tactile and microscopic setae (terminology *sensu* Hinton 1946) and 12 pairs of pores (labrum studied

separately—see below and Fig. 29). Some pores may not be discernible under SEM (Downey & Allyn 1979). Setae AF2, F1, F2, L, and P2 absent. Head setae and pores on first instar larva distributed in ten groups as follows:

Adfrontal (AF) group. Seta AF1 dorsal of tentorial pit and almost touching adfrontal suture. Pore AFa near dorsal angle of frontoclypeus.

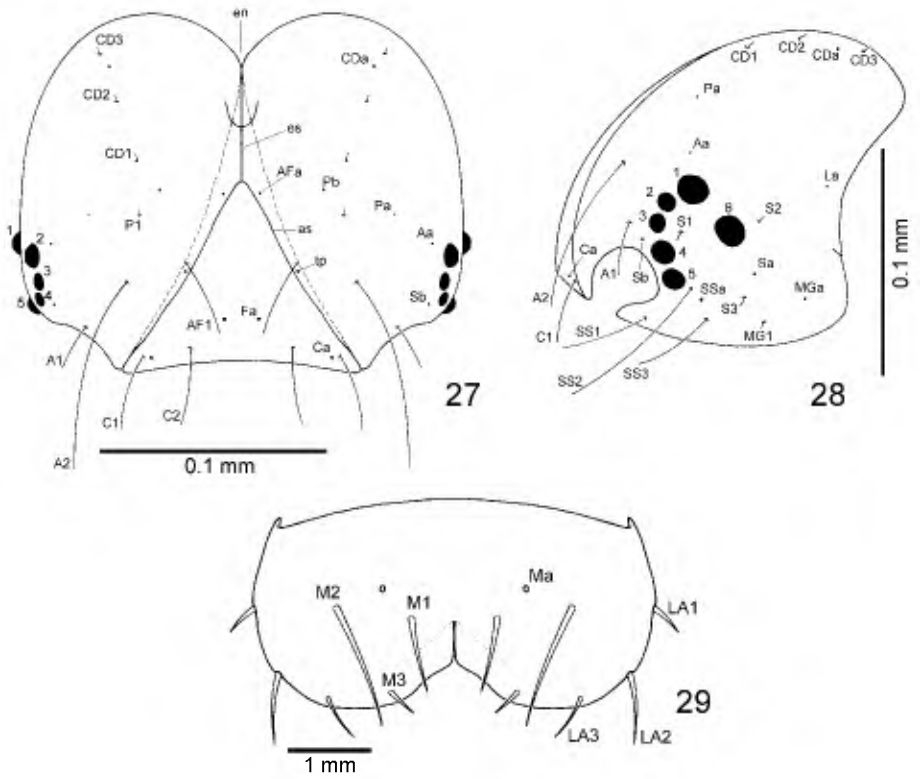
Anterior (A) group. Seta A1 about a fourth length of A2 and more ventral. Pore Aa dorsal of and near stemma 1.

Cephalo-dorsal (CD) group (= microdorsal or MD of some authors). Setae CD1, CD2, and CD3 microscopic, nearly equal in size. On dorsal epicranium. Pore CDa between CD2 and CD3, closer to CD3. The new terminology cephalo-dorsal is adopted in the present paper to avoid confusion with the microdorsal setae of the abdomen.

Clypeal (C) group. C1 and C2 on frontoclypeus area. C1 located laterally near adfrontal suture. C2 located medially closer to midline. C1 and C2 nearly equal in length. Pore Ca near base of C1.

Frontal (F) group. Pore Fa dorsal of C2 and much closer to midline.

Lateral (L) group. No seta. In lateral view, pore La near posterior margin of head.



FIGURES 27–29. *Calycopis caulonia*, head chaetotaxy of first instar larva. 27. Anterior view. 28. Lateral view. 29. Labrum. Abbreviations (for chaetotaxy see text): as, adfrontal suture; en, epicranial notch; es, epicranial suture; tp, tentorial pit.

Microgenal (MG) group. Seta MG1 on lower, rear portion of head. Pore MGa postero-dorsal of MG1.

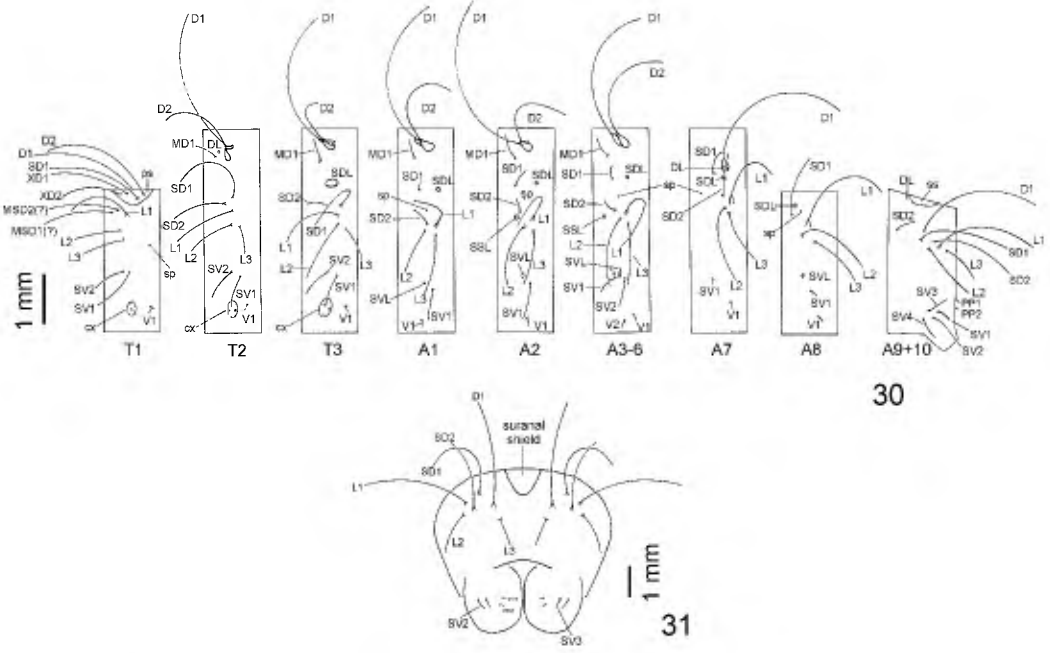
Posteriodorsal (P) group. P1 similar in length to CD setae. Seta P1 with pores Pa and Pb delimiting a triangle. Pa horizontally aligned with P1, and Pb more dorsal of it.

Stemmatal (S) group. Stemmatal setae nearly equal in length, and in lateral aspect, located behind the stemmata (Fig. 28). Seta S1 inside semicircle delimited by stemmata 1–5, level with stemma 3. Setae S2 dorsal of and closer to stemma 6. S3 posterior to stemma 5. Pore Sa between S2 and S3; pore Sb anterior to and between stemmata 3 and 4.

Substemmatal (SS) group. Same number of setae as S group, but setae longer (tactile setae). Setae SS1 and SS3 nearly equal in length, shorter than SS2. SS1 and SS2 closer to antennal socket than SS3. Pore SSa between SS2 and SS3, near base of SS2.

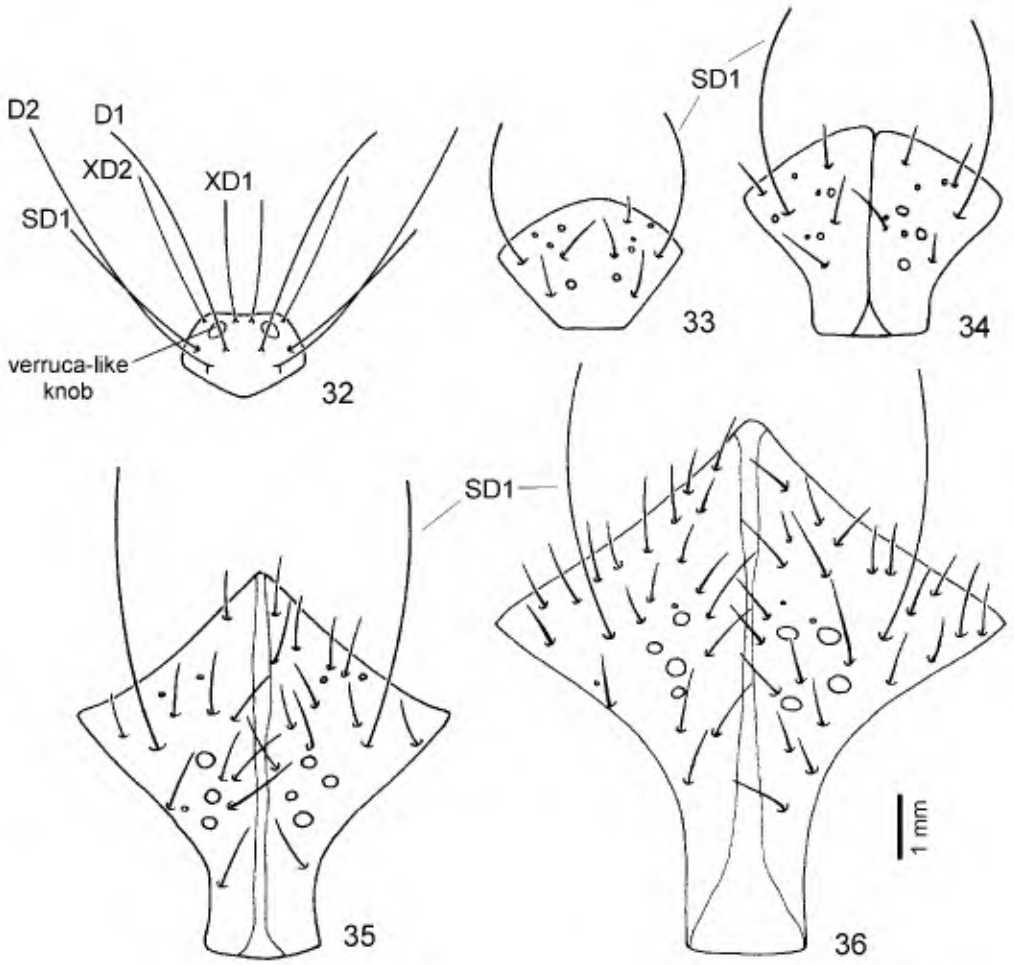
Labrum chaetotaxy (Fig. 29). Labrum of first instar notched with six pairs of primary setae and one pair of pores, distributed as follows: three pairs of medial setae (M1, M2, and M3), M1 slightly shorter than M2 and nearer midline; M3 shortest, nearer ventral margin of labrum; pore Ma (= puncture P *sensu* Peterson 1962) dorsal and equidistant to setae M1 and M2; three pairs of lateral setae (LA1, LA2 and LA3): LA1 dorsal and about half the length of LA2, LA3 most ventral.

Body chaetotaxy (Figs. 30–32, 37–41). 130 pairs of primary setae and 29 pairs of pore cupola organs (PCOs) distributed as follows:

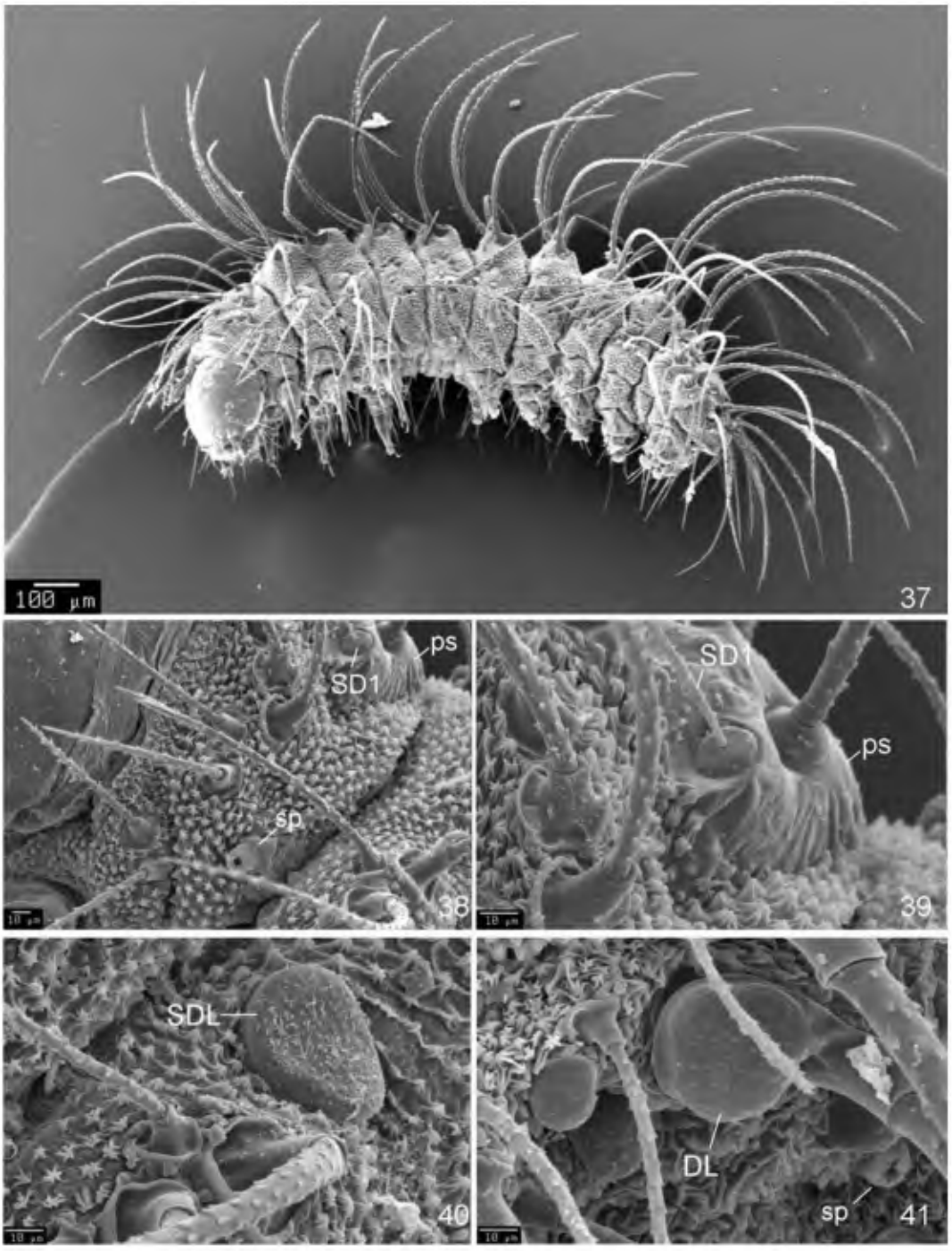


FIGURES 30–31. *Calycopis caulonia*, body chaetotaxy of first instar larva. 30. Dorso-lateral view. 31. Posterior view of the last abdominal segment. Abbreviations (for chaetotaxy see text): A, abdominal segment; cx, coxa; ps, prothoracic shield; sp, spiracle; ss, suranal shield; T, thoracic segment.

Prothorax (Figs. 30, 32, 37–39). Five pairs of setae (XD1, XD2, D1, D2, and SD1—all directed forwards, Fig. 37) and one pair of PCOs (verruca-like knob) on prothoracic shield (Fig. 32). XD1 shorter than XD2, on anterior margin of shield; XD1 closer to midline; XD2 anterior and slightly lateral to a PCO (= lenticle LP of Downey & Allyn 1984b). D1 approximately central on shield, in lateral view (Fig. 30) slightly longer than D2, which is closer to the posterior margin of shield. SD1 (XD2 *sensu* Downey & Allyn 1979) lateral on shield, slender, on a pinaculum rather than a chalaza, present all instars (Figs. 32–36). Setae MSD1, MSD2, L1, L2, L3, SV1, SV2, and V1 on prothorax. MSD1 and MSD2 usually microscopic (Hinton 1946: 16; Stehr 1987: 297, 302), but tactile in first instar of *C. caulonia* (Figs. 30, 37). L1 longer than L2 and L3; L1 and MSD2 very close at their bases; L2 and L3 anterior and dorsal to prothoracic spiracle; L2 and L3 nearly equal in length. SV1 and SV2 ventral of subspiracular fold; SV1 longer. V1 short when present.



FIGURES 32–36. *Calycopis caulonia*, chaetotaxy of prothoracic shield. 32. First instar. 33. Second instar. 34. Third instar. 35. Fourth instar. 36. Fifth instar. Note that the primary seta SD1 is present in all larval instars.



FIGURES 37–41. *Calycopis caulonia*, chaetotaxy of first instar larva. 37. Lateral view. 38. Upper portion of prothorax. 39. Prothoracic shield showing base (pinaculum) of seta SD1. 40. Metathorax showing subdorsal pore cupola organ (= subdorsal lenticle or SDL). 41. Seventh abdominal segment with dorsal pore cupola organ (= dorsal lenticle or DL) joined to the chalaza of seta D1. Abbreviations: ps, prothoracic shield; sp, spiracle.

Mesothorax (Figs. 30, 37). 11 pairs of setae (MD1, D1, D2, SD1, SD2, L1, L2, L3, SV1, SV2, and V1) and one pair of PCOs. MD1 about 1/5 length of D1, close to mid-dorsal line, associated with and mesal to a PCO (DL of Ballmer & Pratt 1992). D1 and D2 posterior to MD1, arching upward and posteriorly (Fig. 37); D1 more dorsal and longer than D2. SD1 and SD2 very close at their base, but SD1 posterior and dorsal to SD2. L2 closer to L3 than L1; L1 dorsal to and longer than L2 and L3. SV1, SV2, and V1 as in previous segment.

Metathorax (Figs. 30, 37, 40). 11 pairs of setae (identical to T2) and one pair of PCOs. Similar to mesothorax. MD1 anterior and ventral to D2. Subdorsal PCO (SDL of Ballmer & Pratt, 1992) large, with tiny punctures (Figs. 30, 40). SD1 as long as D1.

Abdominal segment 1 (Figs. 30, 37). 10 pairs of setae (as on T2, SV2 absent) and two pairs of PCOs. MD1, D1, and D2 identical to previous segment. SD1 shorter, more dorsal, associated with a subdorsal PCO (SDL); SD2 ventral of spiracle. L1 long, L2 and L3 subequal in length. L3 posterior and ventral to L2. SV1 near a subventral PCO (SVL of Ballmer & Pratt 1992).

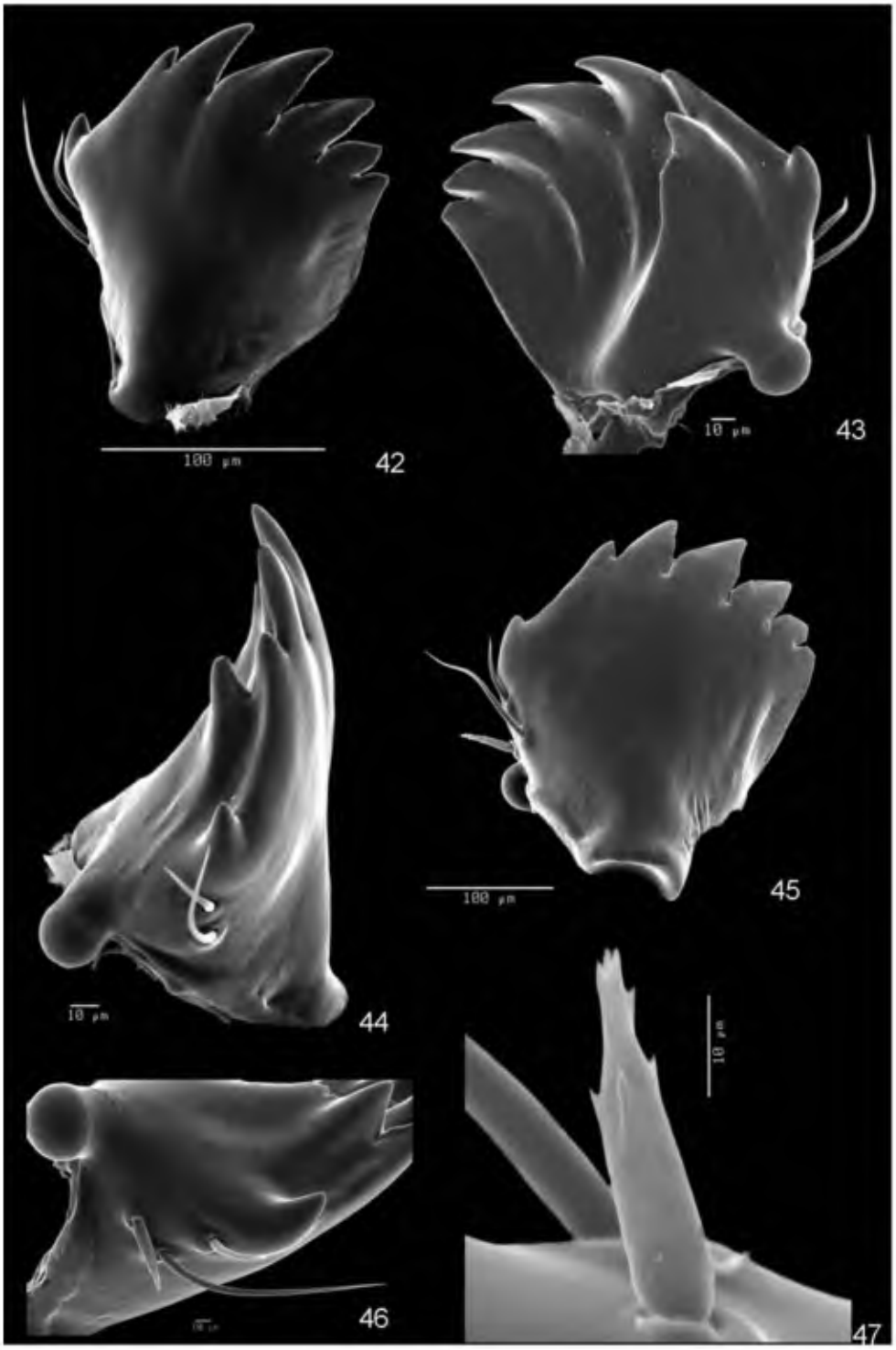
Abdominal segment 2 (Figs. 30, 37). 10 pairs of setae and three pairs of PCOs. Setae and PCOs identical to the previous segment. SD2 now associated with a subspiracular PCO (SSL of Ballmer & Pratt 1992).

Abdominal segments 3–6 (Figs. 30, 37). 12 pairs of setae (D1, D2, MD1, SD1, SD2, L1, L2, L3, SV1, SV2, V1, V2) and four pairs of PCOs. Similar to the previous abdominal segments, but has one more subventral PCO (SVL of Ballmer & Pratt 1992), half the diameter of the other, associated with seta SV1; setae SV2 and V2 present.

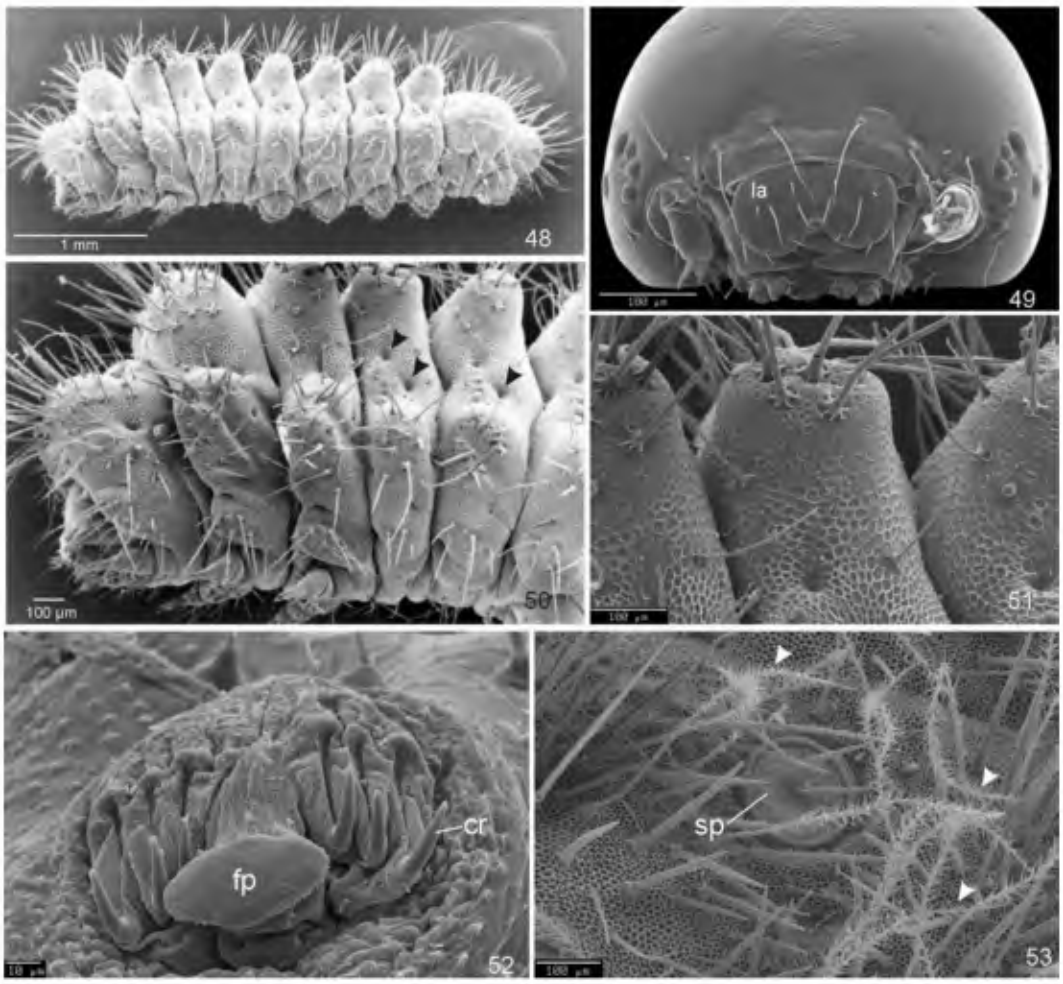
Abdominal segment 7 (Figs. 30, 37, 41). Eight pairs of setae (D1, SD1, SD2, L1, L2, L3, SV1, and V1) and two pairs of PCOs. D1 with a PCO (DL of Ballmer & Pratt 1992), similar to that on subdorsal area of metathorax, joined to its chalaza (Fig. 41). SD2 posterior to and vertically aligned with the spiracle. SV1 shorter than in other segments. V1 identical to previous segments.

Abdominal segment 8 (Figs. 30, 37). Six pairs of setae (SD1, L1, L2, L3, SV1, and V1) and two pairs of PCOs. Setal pattern similar to previous segment, but with seta SD1 longer, anterior to the spiracle, associated with a subdorsal PCO (SDL), and seta SV1 with a subventral PCO anterior and dorsal to it.

Abdominal segments 9+10 (Figs. 30–31). 13 pairs of setae (SD2, D1, SD1, SD2, L1, L2, L3, PP1, PP2, SV1, SV2, SV3, and SV4) and one pair of PCOs. The setal homologies for these abdominal segments are not yet well resolved and should be considered provisional. Suranal plate without setae, anteriorly with a pair of PCOs (DL of Ballmer & Pratt 1992). A9 apparently with only one seta, SD2, level with D1, the longest seta of A9+10. SD1 anterior to D1; SD2 (of A10) posterior and ventral of SD1. L1 posteriodorsal of and longer than L2, L3 shortest and nearer posterior margin. PP1 (nomenclature of Stehr 1987) just ventral of anal slit and dorsal to an extra paraproct seta, PP2. SV1, SV2, SV3, and SV4 subequal in length; SV1 and SV4, respectively, the most posterior and anterior seta of subventral group.



FIGURES 42–47. *Calycopis caulonia*, left mandible morphology. 42. First instar, external view. 43. *Idem*, internal view. 44. *Idem*, ventral view. 45. Fourth instar, external view. 46. *Idem*, ventral view. 47. Detail of the third seta present only on the last two larval instars.

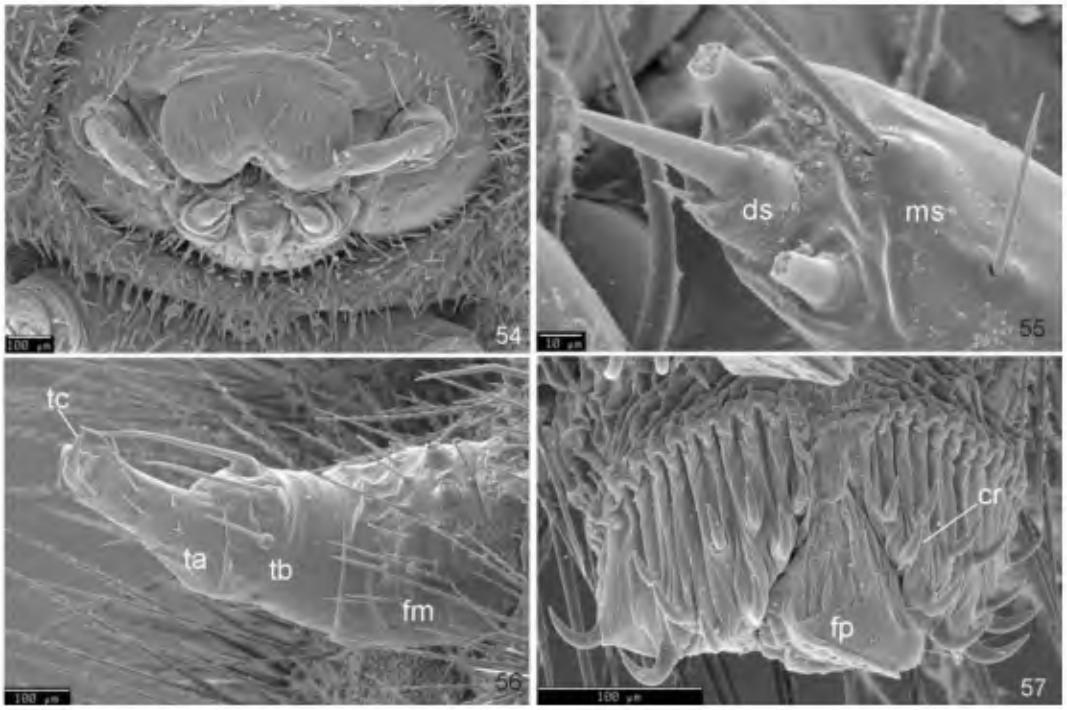


FIGURES 48–53. *Calycopis caulonia*, second and third instar larvae. 48. Body, lateral view. 49. Head, anterior view (see text for labrum chaetotaxy). 50. Detail of integument showing secondary setae distributed radially on dorsal and subspiracular protuberances. Note the uniformly-spaced oval depressions (black arrow heads) scattered over epicuticular surface. 51. Detail of dorsal protuberances and setae. 52. Right proleg of first abdominal segment (uniordinal crochets in uniserial mesoseries). 53. Third instar, dendritic setae (white arrow heads). Abbreviations: cr, crochet; fp, fleshy pad; la, labrum; sp, spiracle.

Second instar (Figs. 20, 33, 48–52). Head translucent, turning dark brown. Labrum and mandibles reddish brown. Primary setae of clypeal, anterior, stemmatal, and substemmatal groups with same distribution and size patterns of the first instar. Secondary setae present. Labrum with three pairs of lateral setae (LA1, LA2, and LA3), four of medial setae (M1, M2, M3, and M4), and two of secondary setae (Fig. 49). LA1 slightly shorter than LA2; LA3 on ventral margin, near median notch of labrum. M1 much nearer the midline than any other seta of labrum, about half the length of M2; M3, the shortest

seta of labrum, about half the length of M1. Mandibles with same number of teeth and setae as first instar. Integument yellowish dorso-laterally, whitish ventrally, with numerous secondary setae distributed radially on dorsal and subspiracular protuberances (Figs. 48, 50–51). Prothorax wider and shorter than other thoracic segments (Figs. 48, 50). Prothoracic shield diamond-shaped, usually with four pairs of setae rather than five (first instar); number and position of setae variable (Fig. 33). A greenish yellow stripe on the dorsal midline from mesothorax to A10, bordered on both sides by a subdorsal reddish stripe; setae absent in intersegmental grooves up to sixth abdominal segment; from seventh to ninth segment this stripe lacking and subdorsal stripes fused, becoming paler gradually. Integument highly sculptured and distinctive, with uniformly-spaced oval depressions scattered over epicuticular surface (Figs. 48, 50–51). Pattern of oval depression similar in remaining instars. Prolegs with uniordinal crochets in uniserial mesoseries, interrupted near center by a conspicuous fleshy pad (Fig. 52), separating the crochets into anterior and posterior groups. Number of crochets variable.

Head capsule width 0.28–0.31 mm (X = 0.29 mm, SD = 0.01, N = 22). Body length 1.68–4.68 mm (X = 3.63 mm, SD = 0.90, N = 9). Duration 3–7 days (X = 4.1 days, SD = 0.9, N= 83).



FIGURES 54–57. *Calycopis caulonia*, larval morphology. 54. Fifth instar larva, anterior view of head partially retracted into prothorax. 55. *Idem*, apex of antenna. Medial segment with two conical papillae supposedly broken. 56. *Idem*, prothoracic leg. 57. Third instar, right proleg of first abdominal segment (triordinal crochets in uniserial mesoseries). Abbreviations: cr, crochet; ds, distal segment; fm, femur; fp, fleshy pad; ms, medial segment; ta, tarsus; tb, tibia; tc, tarsal claw.

Third instar (Figs. 21, 34, 53, 57). Similar to previous instar. Head translucent white, turning dark brown after a few hours; mandibles with same number of teeth and setae as first instar. Color darker because greater number of setae covering most of larval body. Subdorsal reddish stripes paler than previous instar, making dorsal stripe more apparent. Prothoracic shield with same diamond-shape (Fig. 34) and vestigial longitudinal line separating shield in symmetrical parts (Fig. 34). Chaetotaxy of the shield not considered for third instar and following instars because number and placement of setae and PCOs varied intraspecifically. Dendritic setae interspersed with spiculate setae (Fig. 53) on this and later instars. Similarly, crochets of prolegs triordinal, not uniordinal (Fig. 57).

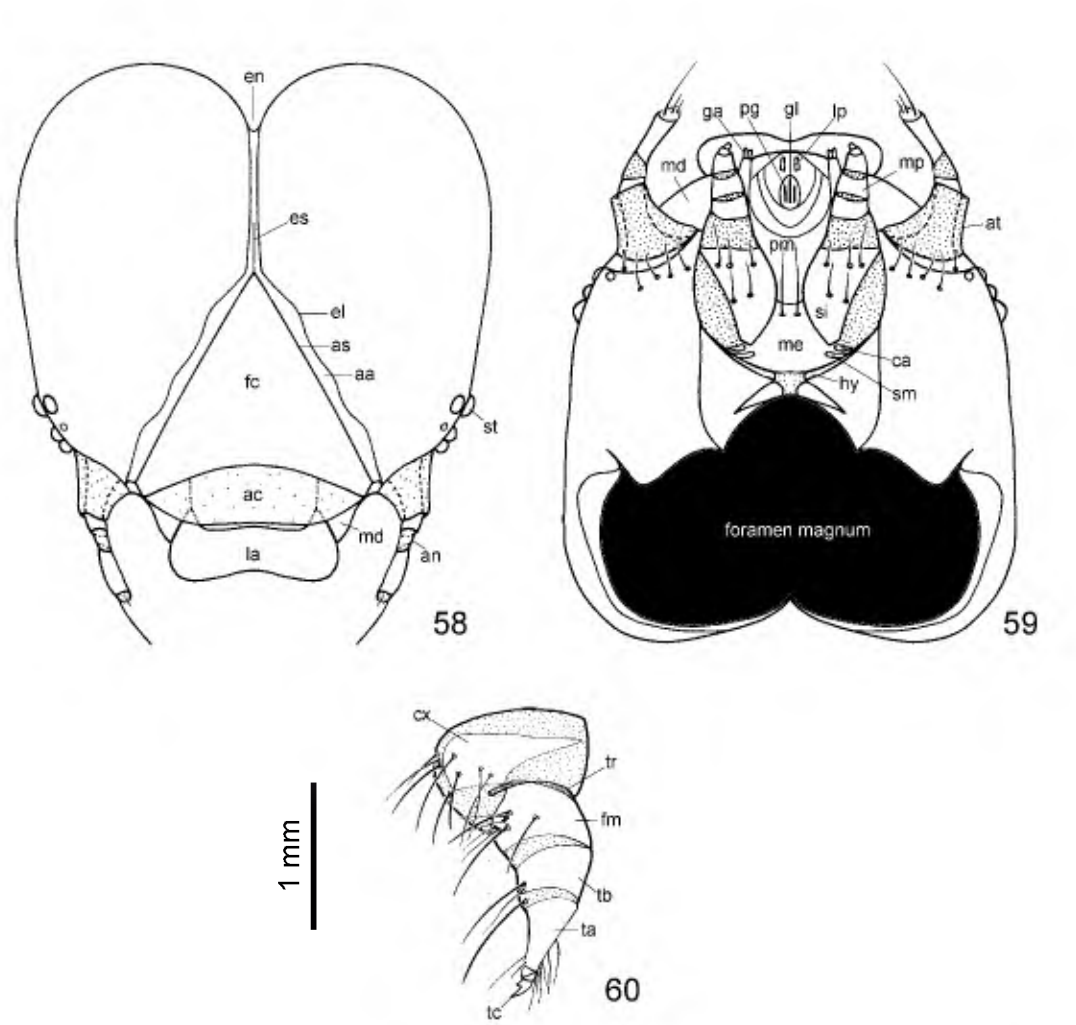
Head capsule width 0.40–0.50 mm (X = 0.43 mm, SD = 0.04, N = 13). Body length 3.96–8.00 mm (X = 5.64 mm, SD = 1.23, N = 7). Duration 3–7 days (X = 4.1 days, SD = 0.9, N = 83).

Fourth instar (Figs. 22, 35, 45–47). Similar to third instar, but greater number of spiculate and dendritic setae (Fig. 22). Mandibles with three setae (Figs. 45–47) rather than two: inner seta, near a rounded condyle, short with minute lateral processes on top (Fig. 47); other mandibular setae, morphologically identical to those of first instar, on ventral margin of mandibles. Prothoracic shield in two symmetrical parts (Fig. 35).

Head capsule width 0.55–0.69 mm (X = 0.62 mm, SD = 0.03, N = 32). Body length 6.25–8.00 mm (X = 7.22 mm, SD = 0.77, N = 10). Duration 4–10 days (X = 6.9 days, SD = 1.2, N = 80).

Fifth instar (Figs. 23–26, 36, 54–56, 58–60). Head, labrum, and mandibles uniform dark brown. Greater number of secondary setae, concentrated on antero-medial region of frontoclypeus (Fig. 54). Adfrontal suture separating frontoclypeus from adfrontal area. Ecdysial line separating epicranium from adfrontal area (cleavage line *sensu* Matsuda 1965) (Fig. 58). Adfrontal area whitish. Mandible strongly sclerotized, same number of teeth and setae as fourth instar. Details of the mouthparts are described only for this instar because they are larger and easier to observe under a microscope. Maxilla well-developed (Fig. 59), comprising the following sclerites: cardo, trapezoidal, articulating basally with submentum, and posteriorly with hypostoma; stipes, lateral plate with setae on anterior two-thirds, joined to anterior part of submentum and lateral of mentum, supporting at distal extremity maxillary palpus (outer) and galea (inner) with series of conical sensilla (Fig. 59). Labium, in ventral aspect, at center of head, delimited anteriorly by mandibles and laterally by maxillae, membranous area with spinneret (Fig. 59) consisting of glossa bordered by paraglossae. Glossa and paraglossae encircled by a circular sclerite (Fig. 59). Labial palpus posterior to spinneret, two-segmented, basal segment large, distal segment cylindrical, with apical setae. Prementum ending anteriorly on hypopharynx, separated from mentum by a narrow membranous area on posterior third. Antenna between base of mandible and stemma 5, three-segmented. Basal segment about 2/3 length of medial segment, inserted in an unmelanized antennal socket (= antacoria, see Hasenfuss & Kristensen 2003: 139). Medial segment with two conical papillae on tip, one protuberance

resembling a seta, and one seta as long as antenna (Fig. 55). Distal segment about ¼ length of basal segment, with a conical papilla and two seta-like protuberances (Fig. 55). Each thoracic segment with a pair of legs. Coxa, slightly sclerotized, setae present; trochanter, narrow blackish sclerite without setae; femur, with setae only on internal surface; tibia, similar to femur in size, with three setae on lower half of internal surface; tarsus with single segment; and pretarsus with non-bifid claw (Figs. 56–57). Prolegs morphologically identical to previous instar, except for number of crochets, but with same distribution and arrangement.



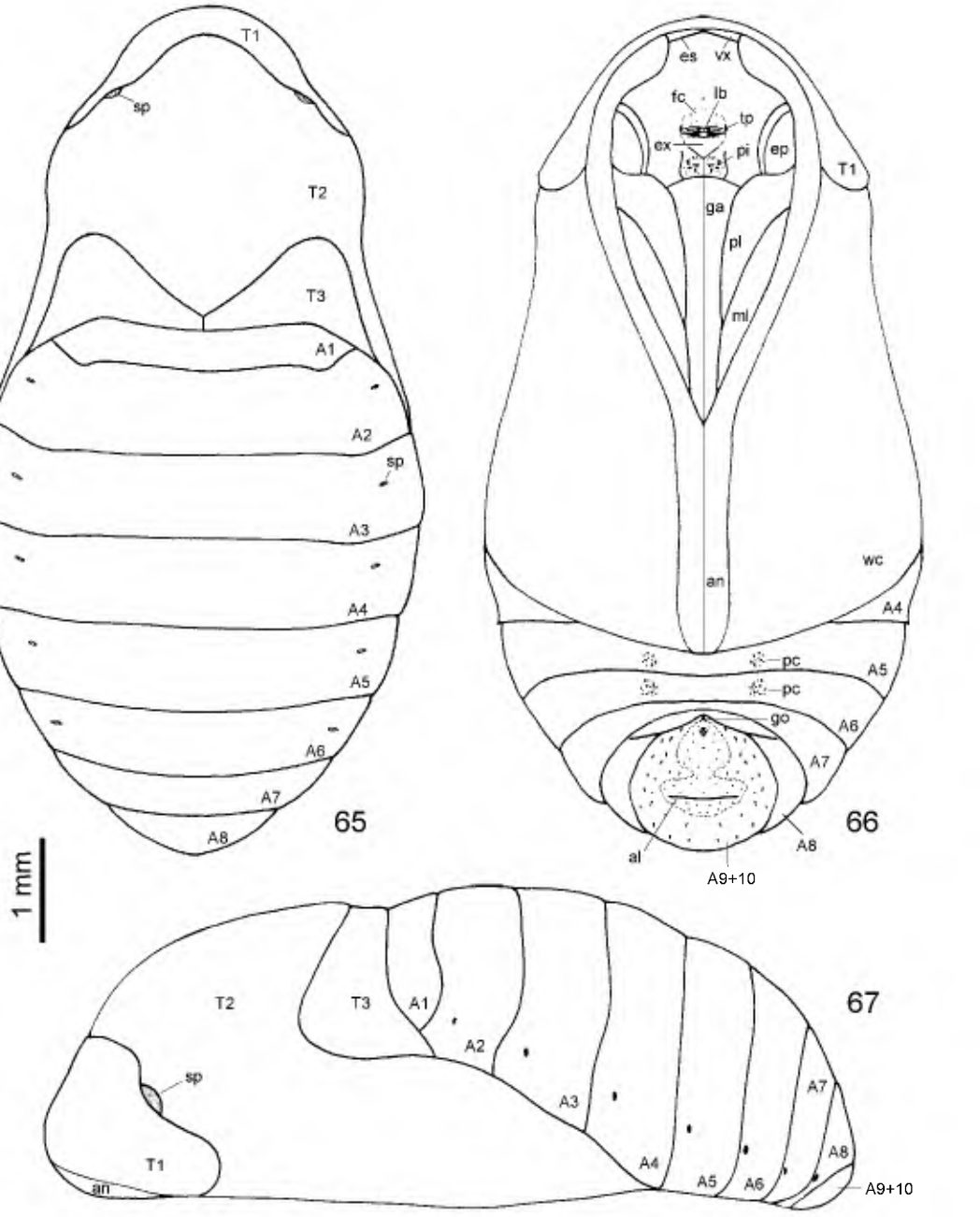
FIGURES 58–60. *Calycopis caulonia*, fifth instar larva. 58. Head, antero-dorsal view. 59. *Idem*, ventral view. 60. Thoracic leg, lateral view. Abbreviations: aa, adfrontal area; ac, anteclypeus; an, antenna; as, adfrontal suture; at, antacoria; ca, cardo; cx, coxa; el, ecdysial line; en, epicranial notch; es, epicranial suture; fc, frontoclypeus; fm, femur; ga, galea; gl, glossa; hy, hypostoma; la, labrum; lp, labial palpus; md, mandible; me, mentum; mp, maxillary palpus; pg, paraglossa; pm, prementum; si, stipes; sm, submentum; st, stemma; ta, tarsus; tb, tibia; tc, tarsal claw; tr, trochanter.

Head capsule width 0.51–0.86 mm (X = 0.75 mm, SD = 0.09, N = 22). Body length

11.25–14.13 mm (X = 12.81 mm, SD = 1.21, N = 10). Duration 8–14 days (X = 10.5 days, SD = 1.3, N = 74).

FIGURES 61–64. *Calycopis caulonia*, pupa. 61. Dorsal view. 62. Dorsal view with darker maculae. 63. Lateral view. 64. Ventral view.

Pupa (Figs. 61–77). Head and thorax initially translucent light green. Abdomen pinkish-white with red maculae from anterior to lateral edges, not reaching spiracles. Finally, light brown, darkening gradually in some individuals. Dark brown maculae scattered on dorsal and lateral body, densely covered with small golden, prominent setae. Wing areas without setae. Head sclerites and appendages fused on ventral surface. Vertex restricted to small area delimited by epicranial suture, antennae bases, and anterior margin of prothorax. Base of antennae about five millimeters from midventral line, dorsal of eye-pieces. Antennae fused posteriorly, concealing the galeae medially, near posterior margin of mesothoracic wings. Frontoclypeus smooth, posterior to epicranial suture and between tentorial pits. Epipharynx subtriangular, anterior to pilifers. Thoracic segments visible only in dorsal and lateral aspects. Ventrally, concealed by thoracic appendages and head. Prothorax poorly delimited. Foreleg adjacent to galea, about 1/3 length of mesothoracic wing. Mesothorax largest, arched dorsally. Midleg posterior to foreleg, approximately same length. Mesothoracic wing with fine reticulations, concealing metathoracic wing and most of ventral surface of segment A4. Thoracic spiracle between prothorax and mesothorax, with lateral opening adjacent to posterior margin of prothorax and external closing plate of somewhat honeycombed appearance (Figs. 68–69). Metathorax weakly developed, laterally limited by mesothoracic wings. Abdomen with 10 segments. Segments



FIGURES 65–67. *Calycopis caulonia*, pupa. 65. Dorsal view. 66. Ventral view. 67. Lateral view. Abbreviations: A, abdominal segment; al, anal slit; an, antenna; ep, eye piece; es, epicranial suture ex, epipharynx; fc, frontoclypeus; ga, galea; go, genital opening; lb, labrum; ml, mesothoracic leg; pc, proleg scar; pi, pilifer; pl, prothoracic leg; sp, spiracle; T, thoracic segment; tp, tentorial pit; vx, vertex; wc, wing case.

A1–9 discernible only in dorsal and lateral aspects. A10 modified to support cremaster ventrally, with short hooked setae (Figs. 73–74). Ventral surface of segments A1–4 completely concealed by wings. Spiracles on segments A1–8; first pair not easily seen; last pair without distinct opening (not functional). Lumina highly elaborated and coral-like (Fig. 70). Externally, bordered by elliptical peritreme (Fig. 70). Pair of proleg scars on segments A5–6 covered by setae, PCOs, and pedunculate discs (most likely 'modified setae' *sensu* Dias 1980), with fungiform appearance (Figs. 71–72). Male with single ventral opening (corresponding to 'ductus ejaculatorius' *sensu* Jackson 1889 in the adult) on posterior margin and midline of segment A9 (Fig. 75). Female with two adjacent genital openings—one on segment A8 (corresponding to 'aperture of bursa copulatrix' *sensu* Jackson 1889), other on segment A9 (corresponding to 'oviduct' *sensu* Jackson 1889) (Fig. 76). A patch of microtrichia (unknown function) posterior to genital openings of male and female pupae (Figs. 75–77).

Pupal width on metathorax 3.0–4.0 mm (X = 3.2 mm, SD = 0.3, N = 24), on segment A3 4.0–6.0 mm (X = 4.8 mm, SD = 0.4, N = 24). Pupal length 7.9–11.1 mm (X = 9.0 mm, SD = 0.8, N = 24). Duration 13–16 days (X = 13.9 days, SD = 0.7, N = 62).

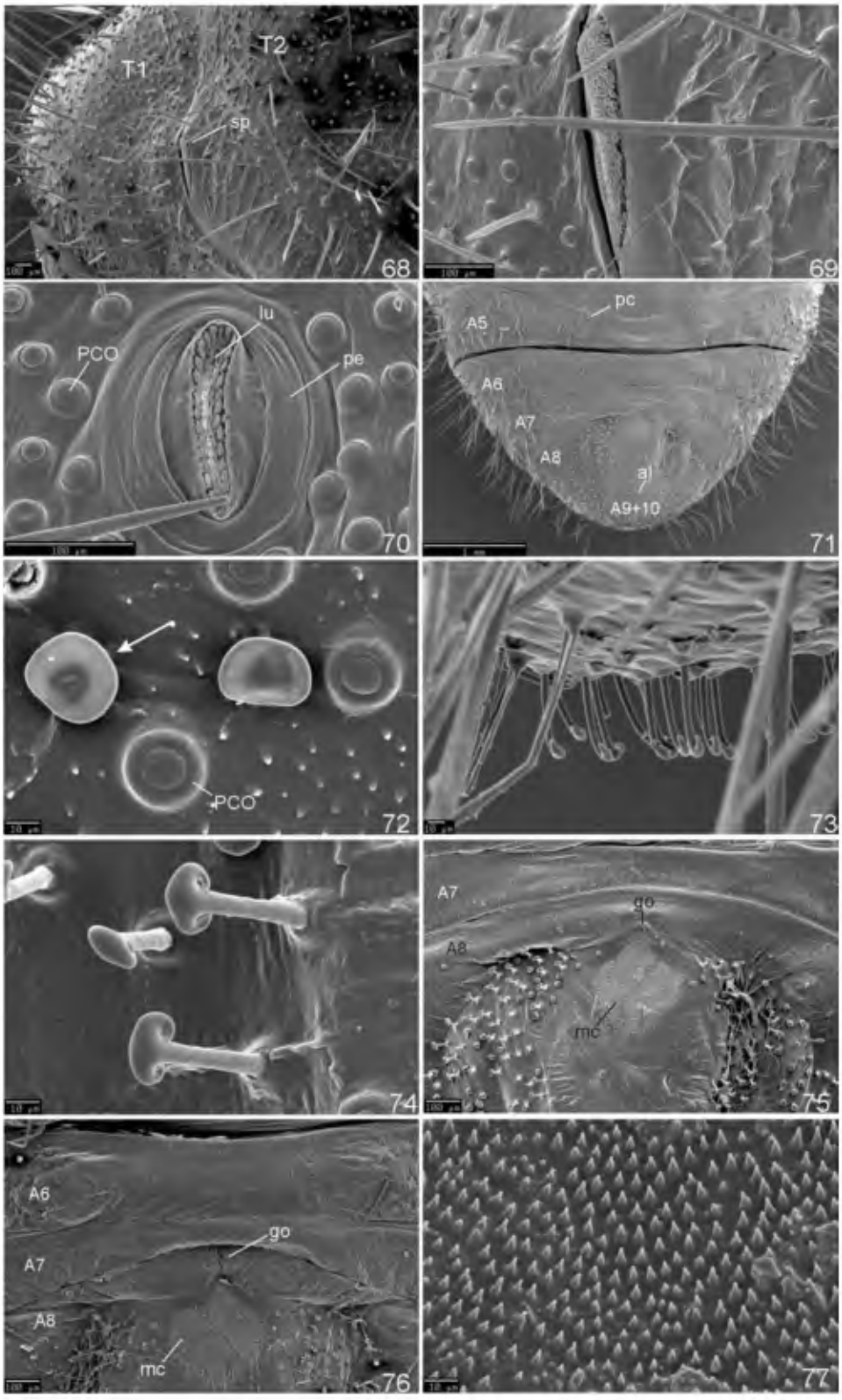
Life cycle of *C. caulonia* on artificial diet

All larval instars fed on artificial diet. Although the quantity of artificial diet consumed by each instar was not measured, second and third instars seemingly consumed the most diet. Fifth instar larvae were also observed eating the damp filter paper placed on the bottom of the rearing containers. Table 2 summarizes data on development times from egg to adult. Females of *C. caulonia* emerged from pupae as adults earlier on average (X = 50.4 days, SD = 2.3) than males (X = 53 days, SD = 2.1).

TABLE 2. Life cycle of *C. caulonia* in laboratory (from egg to adult).

Interval	Duration (days) X	SD	Range (days)	N
Egg to adult	51.4	2.6	46–57	64
Egg to male	53.0*	2.1	49–57	25
Egg to female	50.4*	2.3	46–56	39

* $p<0.05$



FIGURES 68–77. *Calycopis caulonia*, pupa. 68. Lateral view of prothorax (T1) and mesothorax (T2). 69. Thoracic spiracle. 70. Abdominal spiracle. 71. Ventral view of abdominal segments (A5–A10). 72. Detail of a proleg scar showing the presence of pedunculate "seta" (arrow) with fungiform appearance. 73. Cremaster hooks. 74. Details of cremaster hooks. 75. Ventral view of abdominal segments near male genital opening. 76. Ventral view of abdominal segments near female genital openings. 77. Details of the microtrichia patch located below genital openings. Abbreviations: A, abdominal segments; al, anal slit; go, genital opening; lu, lumina; mc; microtrichia patch; pc, proleg scar; PCO, pore cupola organ; pe, peritreme; sp, spiracle; T, thoracic segments.

Discussion

Immatures of *Calycopis caulonia*

Comparison of the morphology of *C. caulonia* immatures with those of other eumaeines is preliminary because of the scarcity of previously published information. Partial life-stage descriptions have been reported for some other eumaeine genera (Healy 1910; Harris 1927; Comstock & Dammers 1935, 1936, 1938; Comstock 1948; Zikán 1956; Ross 1965; Downey 1966, 1987; Downey & Allyn 1973, 1981, 1984a; Callaghan 1982; Brown 1983; Ballmer & Pratt 1988, 1992; Calvo 1998; other references in Bridges 1994 and Lamas *et al.* 1995), but most early publications focus only on general aspects and coloration.

Calycopis caulonia is the first South American species of the genus to have its immature stages described and illustrated. The external morphology of the immatures of *C. caulonia* does not differ significantly from what is known for *C. cecrops* (North American) and *C. isobeon* (Central American) (see Rawson & Hessel 1951; Downey & Allyn 1981; Gifford & Opler 1983; S. Johnson 1985; D. Harvey unpubl.). However, use of an SEM has allowed us to discover some structural features not previously reported that likely will represent synapomorphies at some taxonomic level when information on other species becomes available.

The eggs of *C. caulonia*, *C. cecrops*, and *C. isobeon* possess chorionic sculpturing with elongate and spine-like protuberances (= tubercles *sensu* Downey & Allyn 1981: 9) on the surface except ventrally. This sculpturing is present in other eumaeine genera, such as *Satyrium* Scudder, *Phaeostrymon* Clench, *Lamprospilus* Geyer, *Arumecla* Robbins & Duarte, *Camissecla* Robbins & Duarte, *Strymon* Hübner (Downey & Allyn 1981, 1984a, Duarte unpubl.). Downey and Allyn (1981) distinguished this sculpturing from the "honeycombed group" where ribs predominate instead of tubercles, but noted that the significance of this difference was uncertain because the sculpturing on the eggs of some lycaenid congeners differs greatly.

Downey and Allyn (1981, 1984a) reported difficulty seeing the fine detail of eggs in some SEM preparations, and we encountered similar problems in a small proportion of preparations. Our major difficulty was determining the number of the tiny micropylar openings in the central area of the egg. Downey and Allyn (1981, 1984a) mentioned that dirt may adhere to eggs stored in alcohol or other fixatives and obscure fine detail (for which reason we used ultrasonic cleaning, sometimes unsuccessfully). It is also possible that these difficulties are an artifact of coating specimens for SEM examination.

Our results are the first published chaetotaxy of a *Calycopis* species. The first instar larva of *C. caulonia* is "typical" of the Eumaeini in that cranial setae AF2, F1, F2, L, and P2 are absent (Ballmer & Pratt 1992); there is at least one subdorsal PCO (SDL) in the third thoracic segment and no PCO associated with the lateral group (Ballmer & Pratt 1992). On the other hand, the first instar larva of *C. caulonia* has cranial seta CD3 (=V3 of Ballmer & Pratt 1992), which was previously unrecorded in the Eumaeini.

Ross (1965) was the first to provide notes on the larval chaetotaxy of an eumaeine species, *Eumaeus minijas* (Hübner, [1809]) (= *E. minyas*, cf. Robbins & Lamas 2002). He noted the number and position of setae on the three thoracic segments. The presence of six pairs of setae (two dorsal and four subdorsal) on the first instar *E. minijas* prothoracic shield—rather than five—is uncommon among other eumaeines (Ballmer & Pratt 1992; this study). Ballmer and Pratt (1992) considered five pairs of setae the ancestral condition among "callophryines" (= *Callophrys* Section of Robbins 2004b), as this configuration is widespread among theclines, with some exceptions (Ballmer & Pratt 1992).

Although it had been thought that more than two mandibular setae distinguished the Riodinidae from the Lycaenidae (Downey 1987), Ballmer and Pratt (1988) showed that some lycaenids have more than two mandibular setae. We confirm the findings of Ballmer and Pratt for *C. caulonia*. However, the number of mandibular setae may vary among the instars. The first three instars of *C. caulonia* have two setae, while the others have three setae. Ballmer and Pratt (1988) also found more than two mandibular setae in *Satyrium* Scudder and *Harkenclenus* dos Passos (now synonymized with *Satyrium*—see Robbins 2004b). The other eumaeine genera studied by Ballmer & Pratt (1988)—*Atlides*, *Callophrys*, *Ministrymon*, and *Strymon*—had two setae in the last larval instars. The presence of conspicuous dendritic setae in *C. caulonia* (also present in *C. isobeon, C. bellera,* and *C. vitruvia* (Hewitson), but not in *C. cissusa* (Hewitson)—Duarte 2003; D. Harvey, Duarte and Robbins unpubl.) is another feature shared with *Satyrium*.

We note for the first time the unusual, rather conspicuous pore cupola organs on the larval 7th abdominal segment. It also occurs in *C. isobeon* (D. Harvey, pers. comm.), and it is not yet known at what level this structure may be a phylogenetically informative character.

Life Cycle of *C. caulonia*

Two aspects of the life cycle of *C. caulonia* are unusual. First, female development

time is shorter than male development time (Table 2). This finding is inconsistent with protandry, the common tendency in Lepidoptera for males to emerge before females (Wiklund & Fagerström 1977; Morbey & Ydenberg 2001). Second, *Calycopis caulonia* is the first eumaeine known to have five larval instars. All others have four larval instars (Robbins 1991, unpubl.) except for species of *Callophrys* that feed on Viscaeae or Cupressaceae (Ballmer & Pratt 1988).

Systematics

Calycopis Scudder is the largest genus in the Eumaeini (Robbins 2004b), but is arguably the most poorly resolved taxonomically for a variety of reasons, especially the difficulty of associating males and females (Robbins 2004a). The laboratory rearing methods proposed in this paper may be useful in three distinct ways in resolving the basic taxonomy of *Calycopis*.

The artificial diet rearing method is perhaps the best way to associate *Calycopis* males and females. For example, Field (1967) treated the "South American" *C. devia* (Möschler) as a subspecies (similar male genitalia, distinct wing pattern) of the Central American *C. xeneta* (Hewitson). However, these "subspecies" are sympatric in Panama without any evidence for intergradation. Further, using the rearing method outlined in this paper, Duarte (2003) showed that the female of *C. devia* was different from the female of *C. xeneta* and had been previously described as *C. bellera* (Hewitson), a name that Field had incorrectly identified. For these reasons, *C. xeneta* and *C. bellera* (= *C. devia*) are now treated as different species (Robbins 2004b).

Field (1967) recognized three species in the *C. caulonia* complex in southern Brazil, and K. Johnson and co-authors added another 13 names, mostly from Argentina (Robbins 2004b). Using the artificial diet rearing method under a variety of conditions (humidity, temperature, photoperiod), Duarte (in prep.) reported great variability among siblings of *C. caulonia* reared under different conditions. These differences were similar to those between the previously proposed species.

Perhaps the greatest potential usefulness for the artificial rearing method is that it is an efficient way to obtain sufficient material of preserved immatures to detail their morphology, as we have reported in this paper. The lack of published information with which to compare our results is disappointing, but the wealth of morphological detail that we note bodes well for discovering characters that are phylogenetically informative.

Detritivory & Myrmecophily

Since detritivory was reported in *Calycopis* (S. Johnson 1985), we have observed females of *Lamprospilus*, *Arumecla*, *Ziegleria*, and *Electrostrymon* ovipositing on dead leaves and twigs on the ground (Duarte, Robbins, Aiello, unpubl.). Additionally, larvae of *Calycopis* and these genera have been found eating flowers on the forest floor (Robbins & Aiello 1982, Duarte unpubl., Berkov & Feinstein unpubl.). Finally, we have used the

artificial rearing diet successfully with all of these genera plus *Camissecla* (Duarte, Robbins, Aiello unpubl.). These results increase the likelihood that comparative life history data will be feasible as characters for phylogenetic inference.

Larvae of *Calycopis* have not been reported being tended by ants, as in some eumaeines (recent revision in Pierce *et al.* 2002), and they do not emit "calls" (DeVries 1991a, b). However, as with other non-myrmecophilous lycaenid larvae, they possess PCOs, which are hypothesized to release substances that deter aggression in ants. In addition to the PCOs that are present in all instars and pupa of *C. caulonia*, we also found specialized setae (dendritic setae of Ballmer & Pratt 1988) considered important in maintaining communication between larvae and ants (see Fiedler 1991; Pierce *et al.* 2002). In *C. caulonia* the dendritic setae are present from second to last larval instar, increasing in number with every molt.

Acknowledgements

Francie Chew suggested that we try the artificial diet that she had been using with pierid butterflies and kindly gave us the diet used for this project. Don Harvey discovered that female *Calycopis* could be induced to oviposit in plastic containers with dead leaves. He and Marc Epstein kindly discussed over the years aspects of rearing larvae. In the spirit of cooperation, our colleagues Annette Aiello, Amy Berkov, and Julie Feinstein shared information on detritivorous lycaenids. We received SEM assistance from Susan Braden and Walt Brown (NMNH, Washington D.C., USA), and from Lara Maria Guimarães (MZSP, São Paulo, Brazil). The State of São Paulo Research Foundation (FAPESP) has supported Duarte's research on detritivorous lycaenids (process number 02/ 13898-0 and 03/05895-4) and a research trip by Robbins to São Paulo (process number 03/13985-3). Mirna Martins Casagrande and Danúncia Urban (UFPR, Curitiba, Brazil) read and commented upon the Portuguese version of the manuscript. Dely C. Gomes (Instituto Oswaldo Cruz, Rio de Janeiro, Brazil) permitted reproduction of the map. Guilherme Ide Marques Santos (MZSP) worked with us on some SEM digital images, and Gláucia Marconato (MZSP) illustrated the head capsule (ventral surface) of the fifth instar. John W. Brown and an anonymous reviewer gave valuable suggestions to improve the manuscript. To all, we are greatly indebted and express our thanks.

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